Food Habits of Striped Bass (Morone saxatilis) in Coastal Waters of Massachusetts

Gary A. Nelson, Bradford C. Chase and Jason Stockwell¹

Massachusetts Division of Marine Fisheries, Annisquam River Marine Fisheries Station 30 Emerson Avenue, Gloucester, MA 01930, USA

Abstract

Stomach contents of striped bass (Morone saxatilis) collected from three coastal regions of Massachusetts during June-September in 1997-2000 were examined for patterns in prey composition and body size related to coastal region, time period of capture, foraging habitat, and length of striped bass. Together fish (mostly Clupeidae, Menidia sp., and Ammodytes sp.) and crustaceans (mostly Crangon septemspinosa, Cancer irroratus, and Homarus americanus) dominated the diet of striped bass by both weight (91-95%) and number (87-97%), and had a high frequency of occurrence (42-66%) in the stomachs. Similarity in prey taxa among coastal regions was moderate to high (58-74%). Cluster analysis and ordination techniques grouped the stomach contents from each region by capture period, habitat, and 50 mm striped bass length interval. The stomach contents of bass <675 mm total length (TL) collected during August-September from estuaries and rocky shoreline habitats in the North Shore and Cape Cod Bay regions had a higher average percentage of menhaden (Brevoortia tyrannus) by weight than found in similar-sized bass collected during June-July from the same habitats. Also, in the North Shore area, striped bass ≤675 mm TL sampled in rocky shorelines contained a higher average percentage of Cancer irroratus by weight than similar-sized bass taken in estuaries. Bass ≥675 mm TL in rocky habitats consumed more *Homarus americanus* than smaller bass residing in this same habitat. The size distribution of the dominant fishes and crabs (Ammodytes sp., B. tyrannus, Cancer irroratus, and Carcinus maenus) consumed by striped bass was related to bass body size. Benthic prey were found to be a major component of the diet of striped bass in Massachusetts coastal waters.

Key words: diet composition, Morone saxatilis, prey size, striped bass

Introduction

The striped bass, Morone saxatilis, is a recreationally and commercially important anadromous fish species found along the United States Atlantic coast from Florida to Maine (Setzler et al., 1980). Portions of the adult striped bass stocks in the Chesapeake Bay, Delaware Bay, and the Hudson River migrate in spring and summer to northern feeding grounds along the U.S. continental shelf. In New England, adult striped bass are predominantly female because larger fish migrate farther north and females grow larger than males (Seltzer et al., 1980; Klein-MacPhee, 2002). Records of recreational and commercial total catches (Anon., 2001) indicate that a large proportion of the migrating Atlantic striped bass population seasonally resides in coastal waters of

Massachusetts implying that this area is an important foraging ground.

Little is known about the food habits of striped bass in Massachusetts waters. Bigelow and Schroeder (1953) list the fishes and invertebrates consumed by striped bass in the Gulf of Maine (Cape Cod, Massachusetts to Nova Scotia) and indicate that prey may vary with locality and size of bass. Seasonal changes in diet have been documented for striped bass in Chesapeake Bay (Hartman and Brandt, 1995), but not for fish in coastal feeding grounds. The current study was conducted during the summer of 1997–2000 to examine the food habits of striped bass in Massachusetts's coastal waters. Prey composition was evaluated relative to coastal region, length of striped bass, time period of capture, and foraging habitat.

¹ Present Address: The Jackson Laboratory, Computational Biology Resource, 600 Main Street, Bar Harbor, ME 04609, USA

Methods

Data Collection

Striped bass were collected monthly in Massachusetts territorial waters during June-September from 1997 through 2000. Sampling was concentrated in three coastal regions (North Shore; Cape Cod Bay; Nantucket Sound: Fig. 1) defined a priori to reflect potential differences in prey assemblages. The three regions were delineated using the Cape Cod peninsula as a primary zoogeographic boundary (Briggs, 1974; Ayvazian et al., 1992) and by examining historical catch data from Massachusetts Division of Marine Fisheries (DMF) seine and trawl surveys (e.g., Lawton et al., 1984). The North Shore region exhibits a cold-temperate fauna, while a mixed cold-/warm-temperate fauna characterizes Cape Cod Bay. The Nantucket Sound region possesses a warmtemperate fauna.

Striped bass were collected from four different habitats: estuaries (includes embayments, enclosed harbors and tidal rivers), ocean-facing beaches, rocky shorelines, and offshore waters (ocean >900 m from shore), although not all habitats are available or were sampled in each region. Bass were collected by angling using spinning rods with cut/live natural bait or artificial lures, and by volunteer captains using fly-fishing gear aboard routine fishing charters. Supplemental samples were collected using 76 m, 101 and 127 mm stretched mesh gillnets, and a 150-hook long-line.

After capture, striped bass were immediately placed on ice. In the laboratory, all fish were measured (total length ± 1 mm), weighed (total weight ± 1 g) and sexed. Stomachs were dissected, frozen at -5°C, and processed at a later date. Contents of individual stomachs were sorted, identified to the lowest possible taxon, counted, blotted dry, and weighed collectively to the nearest ± 0.01 g. Fragments of prey organisms were counted as one unless countable parts, such as whole claws, were found. For intact recognizable prey, total length (fish), carapace length (lobster), or carapace width (crabs) was measured (± 1 mm) to subsequently examine the relationship between predator and prey size.

Data Analyses

Dietary analyses were conducted following the protocols advocated by Cortes (1997). Empty stomachs – and contents identified as sampling bait – were eliminated from analysis. For each combination of year,

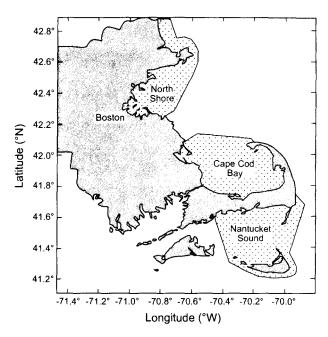


Fig. 1. Map showing boundaries of the three coastal regions of Massachusetts from where striped bass were collected.

month, and habitat, the following indices were calculated for each prey taxon: i) the percentage of stomachs containing prey in which that taxon occurred (frequency of occurrence, F); ii) the number of individuals of that taxon found in all stomachs containing prey, expressed as a percentage of total number of prey (N) obtained from all stomachs with prey; and iii) the total weight of that taxon expressed as a percentage of the total stomach content weight (W) obtained from all stomachs containing prey. Indices of F, N, and W for all levels combined were then calculated by taking the grand mean of each index across all levels.

Stomach contents were examined by 2-month time period, foraging habitat, and striped bass length class. For each region and year, data were pooled into combinations of bimonthly period (June–July and August–September), habitat type, and 50-mm striped bass length intervals. Pooling over two months was required because monthly sample sizes were insufficient to reliably determine diet composition for various period-habitat-length combinations. Indices for each taxon were calculated for each of the four years, and averaged over all years to minimize the effects of inter-annual variability. The 50-mm striped bass length interval was the smallest interval that provided adequate sample sizes to: a) reliably estimate diet composition for each 2-month time period/habitat

combination, and b) detect dietary changes related to fish size. When fewer than five stomachs with prey were available in any period/habitat/length combination, these stomachs were eliminated from analysis due to insufficiently small sample size (and to avoid non-representativeness). Nonparametric multivariate techniques were used to identify and analyze patterns in the stomach contents data. Similarity matrices were constructed using pairwise Bray-Curtis coefficients (Bray and Curtis, 1957) applied to the square-root transformed, percent weight (%W) prey data. Prey weight was used because this metric more closely reflects the energetic importance of prey in the diet than either frequency of occurrence or numerical abundance. Hierarchical agglomerative clustering with group-average linking (Clarke, 1993) was used to identify prey groups in each region across periods, habitats and striped bass length intervals. To corroborate the reliability of the clustering results, nonmetric multidimensional scaling (NMDS) [a multivariate ordination technique (Clarke, 1993)] was used to ordinate the period/habitat/length prey composition data in two dimensions based on similarity matrices. Two-dimensional NMDS ordination is useful in summarizing multidimensional data when the stress value is <0.2 (Clarke and Warwick, 2001). To evaluate the clustering results, cluster definitions were superimposed over the NMDS ordination plot. In those cases where additional groups were ordinated by NMDS within the cluster overlay, or a more defined cluster configuration was identified, the NMDS groupings were adopted [since cluster analysis results can be less reliable where there is a steady change in sample (diet) composition related to large ranges in correlated environmental factors (i.e., size of fish)(Clarke, 1993)]. In addition, pairwise Bray-Curtis similarity coefficients – based on presence/absence of prey - were calculated to determine the similarity of prey taxa consumed by striped bass. All multivariate analyses were conducted with Plymouth Routines in Multivariate Ecological Research (PRIMER) programs (Clarke and Warwick, 2001).

Dietary patterns were elucidated by identifying the prey taxa which contributed most to the separation between clusters and relating these patterns to the main characteristics (i.e., period, length, habitat type and region) of the defined clusters. The similarity percentage (SIMPER) routine (Clarke, 1993; Clarke and Warwick, 2001) was used to calculate the contribution of an individual taxon to the average dissimilarity among clusters. A taxon was considered a reliable discriminator between clusters if the ratio between its

mean contribution and the standard deviation of its mean contribution across all groups was ≥ 1.60 .

Linear regression analysis (Sokal and Rohlf, 1981) was used to evaluate relationships between average prey size and predator length using data from all regions and years combined.

Results

A total of 3 006 striped bass stomachs were collected during the study period: 1 536 from the North Shore, 1019 from Cape Cod Bay, and 451 from Nantucket Sound (Table 1). Of these, 1 720 contained prey: 886 from the North Shore, 614 from Cape Cod Bay, and 220 from Nantucket Sound. Fish sizes ranged from 323 to 1 156 mm ($\bar{x} = 620$ mm) in the North Shore region, from 290 to 1 162 mm ($\overline{x} = 679$ mm) in Cape Cod Bay, and from 305–1 140 mm ($\bar{x} = 675$ mm) in Nantucket Sound (Fig. 2). Most fish were female (83–88%, by region) and were caught between 0600-1159 hours (77-90%, by region). Slightly more than half (57%) of all stomachs collected contained prey, although this varied regionally (49–60%) (Table 1). By fish size, the average percentage of stomachs with prey (over all four years) ranged from 39-53% for striped bass <675 mm, and from 17-38% for bass \geq 675 mm (Fig. 2; Appendix Table 1).

Over 48 prey species representing 55 families from six phyla were found in the stomachs of striped bass (Table 2). Together, fish (Osteichthyes) and crustaceans dominated the diet of striped bass by both weight (91– 95%, by region) and number (87–97%, by region), and had a high frequency of occurrence (42-66% of all stomachs, by region). In the North Shore region, fish (mostly Clupeidae) and crustaceans (mostly Crangon septemspinosa, Homarus americanus, Cancer irroratus and Carcinus maenus) were about equally important by weight (50 vs 45%) but crustaceans dominated by number (55%) and frequency of occurrence (58%) (Table 2). In Cape Cod Bay, fish (mostly menhaden, Brevoortia tyrannus and sand eels, Ammodytes sp.) dominated the diet by weight (58%), number (52%) and frequency of occurrence (66%) (Table 2). In Nantucket Sound, crustaceans (mostly Crangon septemspinosa, Cancer irroratus and Ovalipes ocellatus) were more important prey than fish (mostly Clupeidae, Ammodytes sp., Prionotus carolinus and unidentified Osteichthyes) in terms of weight (53%) and frequency of occurrence (55%) but not by number (40 vs 47%) (Table 2). Echinoderms, insects and reptiles were very minor dietary importance in all regions (Table 2).

TABLE 1. Number of striped bass stomachs collected from each region characterized by year, month, habitat and condition of stomach. *Prey* is the number of stomachs that contained prey, *Empty* is the number of stomachs that were empty, and *Total* is the total number of stomachs collected.

			North Sh	ore	C	ape Cod	Bay	Na	antucket	Sound
Variable	Category	Prey	Empty	Total	Prey	Empty	Total	Prey	Empty	Total
Year	1997	84	140	224	71	43	114	81	43	124
	1998	104	150	254	115	36	151	58	46	104
	1999	298	177	475	341	284	625	44	113	157
	2000	400	183	583	87	42	129	37	29	66
	Total	886	650	1 536	614	405	1 019	220	231	451
Month	June	213	107	320	142	77	219	49	72	121
	July	216	179	395	160	111	271	33	87	120
	August	243	227	470	164	152	316	71	33	104
	September	214	137	351	148	65	213	67	39	106
Habitat	Estuary	176	91	267	372	126	498	129	88	217
	Beach	19	4	23	16	2	18	15	7	22
	Offshore	16	7	23	195	259	454	64	129	193
	Rocky Shore	675	548	1 223	28	9	37	0	0	0
	Other	0	0	0	3	9	12	12	7	19

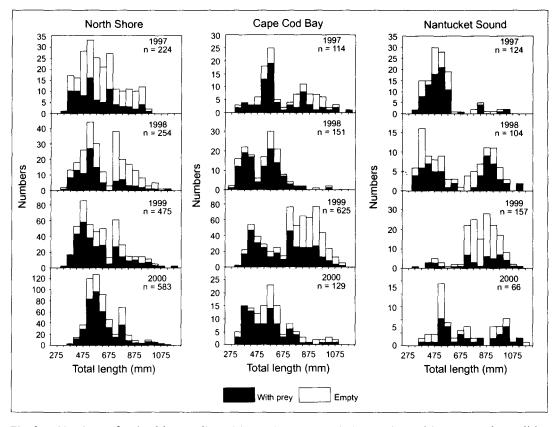


Fig. 2. Numbers of striped bass collected by region, year and size partitioned into stomach condition (empty and with prey).

TABLE 2. Summary of prey items found in stomachs of striped bass, *Morone saxatilis*, from the North Shore, Cape Cod Bay, and Nantucket Sound regions of Massachusetts. W = percent weight, N = percent numerical abundance, and F = percent frequency of occurrence.

		orth Shore rey = 886			Cod Bay (= 614)	,		cket Sour _y = 220)	nd
Taxon	W	N	F	W	N	F	W	N	F
Porifera	<0.1	<0.1	<0.1				Γ		
Nematoda	<0.1	< 0.1	0.3	<0.1	< 0.1	0.6	<0.1	0.2	0.4
Polychaeta	1.4	0.5	3.9	3.7	0.3	5.5	1.7	1.0	3.4
Gastropoda	0.2	0.6	1.2	<0.1	<0.1	0.1	0.1	1.0	3.9
Unidentified Gastropoda	<0.1	<0.1	0.1	10.1	-0.1	0.1	0.1	1.0	3.7
Lacunidae	<0.1	<0.1	0.1						
Littorinidae	<0.1	0.1	0.2	1			<0.1	0.3	0.6
Calyptraeidae	\ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \	٧	٧.٠				"	0.5	0.0
Crepidula fornicata							<0.1	0.7	3.3
Naticidae	ļ						*	0.7	5.5
Neverita duplicata				<0.1	< 0.1	0.1			
Muricidae							1		
Urosalpinx cinerea	<0.1	< 0.1	< 0.1]		
Neptuneidae									
Colus stimpsoni	0.1	0.5	0.6				:		
Nassariidae									
Ilyanassa trivittata	< 0.1	< 0.1	0.1						
Melongenidae	0.1	< 0.1	0.1						
Cephalopoda	1.3	1.5	2.1	2.1	1.1	2.5	3.4	7.9	8.4
Unidentified Cephalopoda	1	1.3	1.6	2.1	1.1	2.3	3.4	7. 9 7.7	8.0
Loliginidae	0.4	1.4	1.0	۷.۱	1.1	2.4	3.3	7.7	8.0
Loligo pealei	0.9	0.1	0.5	<0.1	< 0.1	0.1	0.1	0.2	0.4
	1	0.1		~0.1		0.1	0.1	0.2	
Bivalvia	1.8	0.6	2.5	3.3	3.1	7.9	1.5	1.9	2.4
Unidentified Bivalvia	0.3	0.3	1.6	0.8	2.0	5.7	1.5	1.9	2.4
Mytilidae							l		
Mytilus edulis	1.5	0.3	0.9	0.2	0.8	0.6			
Mactridae									
Spisula solidissima				2.1	0.3	0.8	ļ		
Solenidae									
Ensis directus				0.2	<0.1	0.8			
Crustacea	44.6	55.0	58.3	32.6	42.4	41.8	52.9	40.1	55.0
Unidentified Crustacea	1.3	1.6	7.9	1.2	4.8	4.2	7.4	7.1	9.7
Squillidae							0.3	< 0.1	0.2
Palaemonidae							<0.1	0.1	0.4
Crangonidae									
Crangon septemspinosa	7.7	19.8	19.3	6.6	24.2	20.1	3.9	12.9	9.3
Nephropidae									
Homarus americanus	11.7	3.9	8.2	0.5	0.3	2.0	1.7	1.0	1.8
Paguridae	< 0.1	< 0.1	<0.1	<0.1	0.1	0.4	0.1	0.1	0.4
Majidae	<0.1	< 0.1	< 0.1				0.3	0.2	0.8
Cancridae	1						}		
Cancer borealis	1.3	0.3	1.5	0.1	< 0.1	0.1			, -
Cancer irroratus	14.7	12.1	19.7	10.5	7.9	11.1	5.7	2.5	4.3
Portunidae	1							0.2	6.0
Callinectes sapidus		2 ^	11.0	2.0			0.5	0.3	0.9
Carcinus maenus	6.8	3.0	11.0	3.9	1.8	5.7	4.4	1.9	3.8
Ovalipes ocellatus				9.7	3.1	5.9	18.9	10.6	17.4
Mysidae	-0.1	-C 1	ا م	0.1	-O 1	0.3	1 .	0.3	0.7
Unidentified Mysidae	<0.1	<0.1	0.5	0.1	<0.1	0.3	0.1	0.3	0.7
Neomysis americana	0.1	< 0.1	0.6				l		

TABLE 2. (Continued). Summary of prey items found in stomachs of striped bass, *Morone saxatilis*, from the North Shore, Cape Cod Bay, and Nantucket Sound regions of Massachusetts. W = percent weight, N = percent numerical abundance, and F = percent frequency of occurrence.

	Nor	th Shore		Cap	pe Cod I	Вау	Nant	ucket So	und
Taxon	W	N	F	W	N	F	W	N	F
Idoteidae									
Unidentified Idoteidae	<0.1	<0.1	0.4	<0.1	<0.1	0.1	0.1	0.2	0.7
Chiridotea coeca	}			<0.1	<0.1	0.1	ł		
Idotea baltica	0.1	2.6	3.4	<0.1	<0.1	0.5	<0.1	< 0.1	0.1
ldotea phosphorea	<0.1	< 0.1	0.6						
Unidentified Amphipoda	0.7	2.9	5.9	<0.1	0.2	0.6	5.5	2.8	5.9
Aoridae	<0.1	<0.1	<0.1						
Calliopiidae	<0.1	0.1	0.2				İ		
Gammaridae			• •	l					
Unidentified Gammaridae	0.1	4.7	2.0	<0.1	<0.1	0.3	0.8	<0.1	3.6
Gammarellus angulosus	<0.1	0.1	0.2					.0.1	2.2
Gammarus lawrencianus		.0.1	0.3	l			3.3	<0.1	3.3
Hyalidae	<0.1	<0.1	0.3						
Photidae	<0.1	0.1	0.8						
Ischyroceridae	<0.1	<0.1	0.5				i		
Caprellidae	<0.1	<0.1	0.1						
Insecta	< 0.1	0.1	0.3	İ			<0.1	0.2	0.5
Echinodermata	0.1	0.1	0.1	0.4	1.2	1.5	<0.1	0.1	0.2
Strongylocentrotidae									
Strongylocentrotus droebachiensis	0.1	0.1	0.1	}			ļ		
Echinarachniidae									
Echinarachnius parma				0.4	1.2	1.5	<0.1	0.1	0.2
Chondrichthyes	}						0.1	0.3	0.8
Rajidae							0.1	0.3	0.8
Osteichthyes	50.4	41.6	53.9	57.9	51.8	65.7	40.3	47.1	53.7
Unidentified Osteichthyes	6.8	7.3	15.7	9.0	8.3	18.7	7.3	11.9	15.4
Myxinidae									
Myxine glutinosa	< 0.1	< 0.1	< 0.1	!					
Anguillidae				ĺ			ĺ		
Anguilla rostrata							0.5	0.3	0.6
Clupeidae						*`.	ł		
Unidentified Clupeidae	2.4	5.8	3.8	2.1	5.3	9.2	1		
Alosa sp.	0.7	0.2	0.6	1.3	0.2	1.0			
Clupea harengus	5.8	1.0	3.4	0.1	< 0.1	0.2			
Brevoortia tyrannus	22.6	19.9	21.2	17.2	12.0	17.7	5.5	4.1	5.2
Osmeridae							ļ		
Osmerus mordax	1.0	0.6	1.0]		
Gadidae									
Unidentified Gadidae	0.2	0.3	0.6	0.3	0.9	1.8			
Urophycis chuss	< 0.1	<0.1	0.3	ļ					
Pollachius virens	0.7	0.1	0.3				[
Merluccius bilinearis	0.2	0.2	0.8	2.0	1.9	1.6	1		
Cyprinodontidae]		
Fundulus heteroclitus				0.3	0.1	0.1	<0.1	<0.1	0.2
Atherinidae	, .		2.0			4.5	١		4.
Menidia sp.	1.4	1.3	2.0	0.8	1.5	4.3	1.1	1.3	4.1
Gasterosteidae							0.5	2.2	0.8
Syngnathidae		0.1	0.3	0.3	0.	0.4		0.1	0.3
Syngnathus fuscus	<0.1	0.1	0.2	0.2	0.1	0.4	<0.1	0.1	0.3
Triglidae					1 7	2 1			
Unidentified Triglidae				1.2	1.7	3.1	1 .	2.2	<i>5 -</i>
Prionotus carolinus				1.9	0.9	3.1	7.6	3.2	5.5
Prionotus evolans	Щ			0.2	0.1	1.6	L		

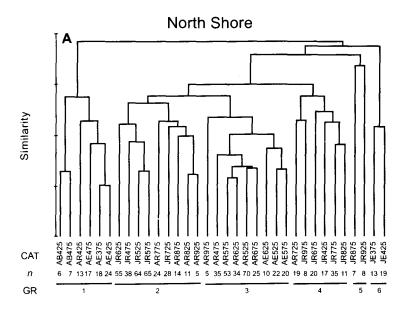
TABLE 2. (Continued). Summary of prey items found in stomachs of striped bass, *Morone saxatilis*, from the North Shore, Cape Cod Bay, and Nantucket Sound regions of Massachusetts. W = percent weight, N = percent numerical abundance, and F = percent frequency of occurrence.

	Nortl	h Shore		Cape	Cod Bay		Nant	ucket	Sound	
Taxon	W	N	F	W	N F		W	N	F	
Cottidae				1			\top			
Unidentified Cottidae	0.2	0.5	0.6							
Hemitripterus americanus				< 0.1	< 0.1	<0.1	0	.4	0.1	0.2
Myoxocephalus sp.	1.4	0.5	1.5	< 0.1	< 0.1	0.1	<	0.1	0.1	0.2
Pomatomidae				1						
Pomatomus saltatrix	<0.1	<0.1	0.2	< 0.1	<0.1	0.1				
Sparidae				1						
Stenotomus chrysops	0.3	<0.1	0.2	1.3	2.5	2.7	3	.4	3.2	5.4
Sciaenidae				1			-			
Micropogonias undulatus				0.8	< 0.1	0.1				
Labridae										
Unidentified Labridae	<0.1	< 0.1	< 0.1	1						
Tautogo onitis	< 0.1	< 0.1	< 0.1	1			0	.1	0.3	0.6
Tautogolabrus adspersus	0.8	0.2	0.8	2.0	0.7	0.9				
Zoarcidae										
Macrozoarces americanus	1.8	0.3	0.9							
Pholidae				ì			1			
Pholis gunnellus	1.0	0.8	1.7	0.1	< 0.1	0.1				
Ammodytidae				1						
Ammodytes sp.	1.3	1.3	2.5	15.8	14.8	21.0	13	3.9	19.6	21.7
Scombridae				ĺ			1			
Scomber scombrus	1.6	0.7	1.5	0.4	0.1	0.1				
Stromateidae										
Peprilus triacanthus	0.1	0.2	0.3	0.3	0.4	1.7	<	0.1	0.7	0.6
Pleuronectidae				1						
Pseudopleuronectes americanus	0.1	0.3	1.1	0.3	0.1	0.5				
Scophthalmidae										
Scophthalmus aquosus				0.1	0.1	0.1				
Tetraodontidae										
Sphoeroides maculatus				0.1	< 0.1	0.1				
Reptilia	0.1	< 0.1	0.2		**					

Bray-Curtis coefficients indicated that similarity in taxa was moderate to high across all three regions (North Shore vs Cape Cod Bay: 74%; North Shore vs Nantucket Sound: 58%; Cape Cod Bay vs Nantucket Sound: 67%). Prey items common to all regions were nematodes, polychaetes, Loligo pealei, Crangon septemspinosa, H. americanus, pagurids, Cancer irroratus, Carcinus maenus, mysids, Idotea baltica, B. tyrannus, Menidia sp., Syngnathus fuscus, Myoxocephalus sp., Stenotomus chrysops, Ammodytes sp. and Peprilus triacanthus (Table 2).

Cluster analysis grouped the stomach contents of 34, 25 and 14 time/habitat/striped bass length categories in the North Shore, Cape Cod Bay, and Nantucket Sound

regions, respectively, into 3 to 6 main clusters linked at similarity levels ranging between 8 and 24% (Fig. 3, 4 and 5). In the North Shore region, six clusters were obtained. Clusters 1 and 6 represent the prey composition of smaller striped bass (375–475 mm TL) caught in estuarine habitats during August–September and June–July, respectively (Table 3, Fig. 3). Clusters 2, 3, 4 and 5 all reflect the prey of striped bass collected from rocky habitats but differ with respect to time (June–July for clusters 2 and 5; August–September for cluster 3; June–September for cluster 4) and fish size (smaller bass in clusters 2 and 3, larger bass in clusters 4 and 5) (Table 3, Fig. 3b). In Cape Cod Bay, the stomach contents of bass grouped into four clusters (Table 4; Fig. 4). Clusters 1 and 2 reflect the prey of estuarine-



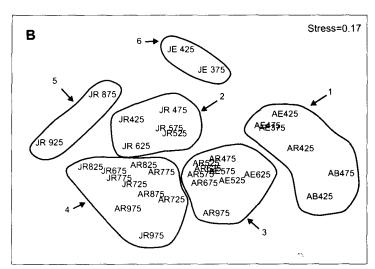
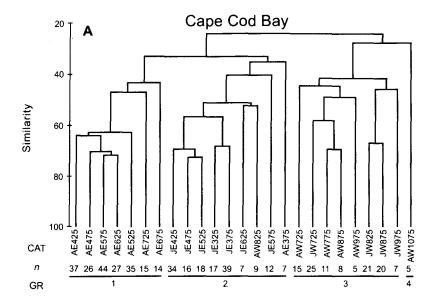


Fig. 3. a) Dendrogram from the cluster analysis (CAT is the point label, n is the number of stomach with prey, and GR is the cluster number) and b) non-metric multidimensional scaling (NMDS) ordination showing similarities in diet among North Shore striped bass. The first letter of dendrogram and NMDS point labels represents the summer period (J = June-July and A = August-September), the second letter respresents the habitat (E = estuary, R = rocky shoreline, and B = beach), and the three digits represent the midpoint of the 50 mm length class. The horizontal bars below the dendrogram show the principal clusters discussed in the text. The circled groups and arrow labels in the NMDS ordination are the cluster groups overlaid onto the plot.

caught bass taken in August-September and June-July, respectively, while clusters 3 and 4 represent the stomach contents of bass collected in offshore, oceanic waters. The latter two clusters differ by time period (Both vs August-September) and size of bass (725-

975 mm vs 1 075 mm). In Nantucket Sound, three prey composition clusters were derived (Table 5, Fig. 5). Clusters 1 and 3 each represent the prey of estuarine-caught bass, but Cluster 3 is based on only five small fish (325 mm TL) sampled during June–July. Cluster 2



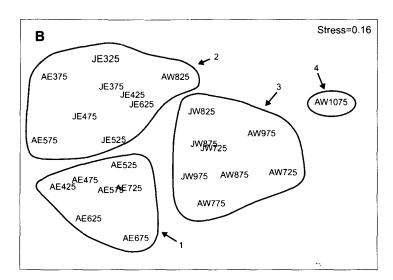
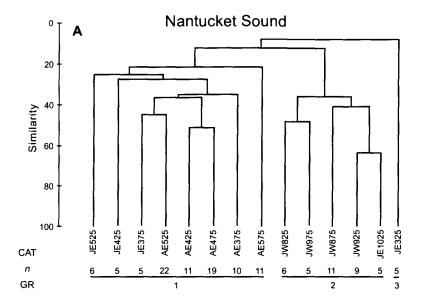


Fig. 4. a) Dendrogram from the cluster analysis (CAT is the point label, n is the number of stomach with prey, and GR is the cluster number) and b) non-metric multidimensional scaling (NMDS) ordination showing similarities in diet among Cape Cod Bay striped bass. The first letter of dendrogram and NMDS point labels represents the summer period (J = June-July and A = August-September), the second letter respresents the habitat (E = estuary and W = offshore), and the three digits represent the midpoint of the 50 mm length class. The horizontal bars below the dendrogram show the principal clusters discussed in the text. The circled groups and arrow labels in the NMDS ordination are the cluster groups overlaid onto the plot.

reflects the stomach contents of large bass (825–1 025 mm TL) taken offshore in June and July.

Comparison of diet compositions among the clusters revealed some consistent patterns. Regardless of habitat type, *Crangon septemspinosa*, *Ammodytes*

sp., and polychaetes were generally consumed by ≤625 mm bass in June–July (North Shore: clusters 2 and 6; Cape Cod Bay: cluster 2), while *B. tyrannus*, *Carcinus maenus*, and *Menidia* sp. were regularly consumed by similarly-sized bass during August–September (North Shore: clusters 1 and 3; Cape Cod Bay: cluster 1;



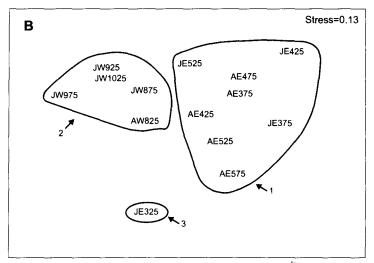


Fig. 5. a) Dendrogram from the cluster analysis (CAT is the point label, n is the number of stomach with prey, and GR is the cluster number) and b) non-metric multidimensional scaling (NMDS) ordination showing similarities in diet among Nantucket Sound striped bass. The first letter of dendrogram and NMDS point labels represents the summer period (J = June-July and A = August-September), the second letter respresents the habitat (E = estuary and W = open ocean), and the three digits represent the midpoint of the 50 mm length class. The horizontal bars below the dendrogram show the principal clusters discussed in the text. The circled groups and arrow labels in the NMDS ordination are the cluster groups overlaid onto the plot.

Nantucket Sound: cluster 1) (Tables 3–5). Regardless of habitat type and period, *Cancer irroratus* was a major prey item of ≥425 mm striped bass (North Shore: clusters 2, 3, 4 and 5; Cape Cod Bay: clusters 1, 2 and 3; Nantucket Sound: clusters 1 and 2) (Tables 3–5).

Irrespective of time period, Crangon septemspinosa and Carcinus maenus were important prey of ≤675 mm striped bass collected in estuaries and beaches (North Shore: clusters 1 and 6; Cape Cod Bay: clusters: 1 and 2; Nantucket Sound: cluster 1) (Tables 3–5).

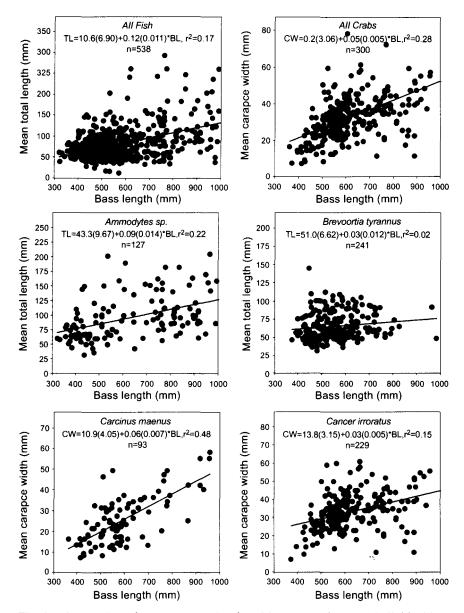


Fig. 6. Regression of average prey size found in a stomach versus individual bass size for all fish combined, all crabs combined, and dominant prey. The regression equations, r-square values, and sample sizes (n) are shown. Standard error of parameters are given in parentheses.

The SIMPER results revealed that the dissimilarities among the clusters were generally due to one to three prey taxa being absent or comprising a large percentage of the diet (Tables 3–5; Table 6). The stomach contents of \leq 675 mm bass collected during August-September from estuarine/beach and rocky habitats in the North Shore (clusters 1 and 3) and Cape Cod Bay (cluster 1) regions had higher percentages (by weight) of *B. tyrannus* than the stomach contents

of similarly-sized bass collected during June-July from the same habitats (North Shore: cluster 2 and 6; Cape Cod Bay: cluster 2). These findings suggest that predation by bass on *B. tyrannus* is time dependent (Table 6). In the North Shore region, higher percentages of *H. americanus* were found in the diets of 675-975 mm striped bass from rocky areas (clusters 4 and 5) than in the diets of smaller bass from the same habitat (clusters 2 and 3), regardless of time period.

TABLE 3. Percent weight-of-prey items found in the stomachs of striped bass of each defined cluster with associated cluster characteristics from the North Shore region. n_{prey} is the number of stomachs with prey.

Cluster	1	2	3	4	5	6
Period	Aug-Sep	Jun-Jul	Aug-Sep	Both	Jun-Jul	Jun-Jul
Habitat	Estuary*	Rocky	Rocky**	Rocky	Rocky	Estuary
Size Interval Range (mm)	375-475	425-625	475-975	675-975	875-925	375-425
ⁿ prey	85	239	274	175	15	32
Taxon			Percer	nt Weight		
Porifera	0.00	0.09	0.00	0.00	0.00	0.00
Polychaeta	0.31	3.11	0.04	4.30	18.70	2.06
Gastropoda	0.00	0.06	0.00	0.40	0.00	0.00
Cephalopoda	0.00	2.48	1.00	0.61	0.00	0.00
Bivalvia	0.10	0.09	0.02	3.47	0.00	2.36
Crustacea						
Unidentified Crustacea	0.33	3.57	1.89	1.04	0.27	0.10
Crangon septemspinosa	15.65	0.87	0.32	0.01	0.02	55.32
Homarus americanus	0.00	13.63	8.54	31.00	47.98	0.00
Majidae	0.00	0.00	0.00	0.03	0.00	0.00
Cancer irroratus	1.15	31.83	27.04	16.98	1.24	0.00
Cancer borealis	0.00	2.63	1.10	1.34	1.77	0.00
Carcinus maenus	3.49	2.74	4.72	5.32	0.70	10.32
Mysidae	4.08	0.00	0.00	0.00	0.00	0.02
Isopoda	0.10	0.59	0.03	0.01	0.00	0.00
Amphipoda	0.88	4.65	0.58	0.12	0.00	3.49
Insecta	0.01	0.00	0.00	0.00	0.00	0.00
Echinodermata						
Strongyl. droebachiensis	0.00	0.00	0.00	0.41	0.00	0.00
Osteichthyes					0.00	4.50
Unidentified Osteichthyes	4.81	4.66	5.61	10.23	0.00	4.59
Myxine glutinosa	0.00	0.00	0.00	0.00	14.35	0.00
Unidentified Clupeidae	0.94	0.74	4.88	1.75	0.00	6.87
Alosa sp.	0.00	6.31	0.00	0.00	0.00	1.57
Clupea harengus	0.00	0.59	0.00	6.24	8.28	6.29
Brevoortia tyrannus	43.40	0.00	37.10	0.92	0.00	0.00
Osmerus mordax	0.00	15.01	0.00	0.75	0.00	0.00
Pollachius virens	0.00	0.00	0.00	1.80	5.48	0.00
Merluccius bilinearis	0.00	1.21	0.03	0.09	0.00	0.00
Urophycis chuss	0.00	0.00	0.03	0.00	0.00	0.00
Menidia sp.	10.20	0.99	0.36	0.00	0.00	0.00
Syngnathus fuscus	0.00	0.18	0.00	0.00	0.00	0.00
Cottidae	0.00	0.25	0.00	0.87	1.22	5.22
Pomatomus saltatrix	0.01	0.00	0.02	0.00	0.00	0.00
Labridae	0.00	0.28	1.19	0.00	0.00	0.00
Macrozoarces americanus	0.00	0.00	0.00	7.21	0.00	0.00
Pholis gunnellus	0.00	2.25	5.23	0.11	0.00	0.00
Ammodytes sp.	12.92	0.62	0.04	0.11	0.00	1.79
Scomber scombrus	0.00	0.08	0.00	3.62	0.00	0.00
Peprilus triacanthus	0.00	0.00	0.19	0.12	0.00	0.00
Stenotomus chrysops	0.00	0.45	0.00	1.15	0.00	0.00
Pleuronectidae	1.61	0.00	0.04	0.00	0.00	0.00

^{*}contains some bass from beach and rocky shorelines; ** contains some bass from estuaries.

TABLE 4. Percent weight of prey items found in the stomachs of striped bass of each defined cluster and their main characteristics from the Cape Cod Bay region. n_{prey} is the number of stomachs with prey.

Cluster	1	2	3	4
Period(s)	Aug-Sep	Jun-Jul	Both	Aug-Sep
Habitat	Estuary	Estuary*	Ocean	Ocean
Size Interval Range (mm)	425-725	325-825	725-975	1 075
n_{prey}	198	159	112	5
Taxon		Percent '	Weight	
Polychaeta	0.18	24.81	0.40	0.00
Gastropoda	0.00	0.00	0.00	0.00
Cephalopoda	1.82	5.61	0.67	0.00
Bivalvia	1.14	2.13	18.03	0.00
Crustacea				
Unidentified Crustacea	0.01	2.08	3.56	0.00
Crangon septemspinosa	2.10	23.83	0.28	0.00
Homarus americanus	0.02	0.04	2.17	0.00
Paguridae	0.05	0.15	0.00	0.00
Cancer irroratus	15.85	8.37	13.52	0.00
Cancer borealis	0.00	0.00	0.84	0.00
Carcinus maenus	5.42	7.86	0.53	0.00
Ovalipes ocellatus	1.30	3.82	13.46	57.58
Mysidae	0.00	0.00	0.05	0.00
Isopoda	0.01	0.03	0.00	0.00
Amphipoda	0.00	0.15	0.00	0.00
Echinodermata				
Echinarachnius parma	0.00	0.00	0.30	8.80
Osteichthyes				
Unidentified Osteichthyes	3.47	4.55	8.71	0.28
Unidentified Clupeidae	5.57	0.27	0.22	0.00
Alosa sp.	1.45	5.27	0.00	0.00
Clupea harengus	0.13	0.19	0.00	0.00
Brevoortia tyrannus	52.89	2.79	0.07	0.00
Unidentified Gadidae	0.00	0.00	3.00	0.00
Merluccius bilinearis	0.00	0.00	18.79	0.00
Fundulus heteroclitus	0.00	0.93	0.00	0.00
Menidia sp.	3.85	0.50	0.00	0.00
Syngnathus fuscus	0.31	0.00	0.00	0.00
Triglidae	0.00	0.00	2.66	33.33
Pomatomus saltatrix	0.08	0.00	0.00	0.00
Labridae	0.03	0.00	0.00	0.00
Ammodytes sp.	1.56	5.30	10.88	0.00
Scomber scombrus	0.00	0.00	1.28	0.00
Peprilus triacanthus	1.51	0.00	0.15	0.00
Sphoeroides maculatus	0.64	0.00	0.00	0.00
Stenotomus chrysops	0.50	0.00	0.00	0.00
Pleuronectidae	0.12	1.33	0.00	0.00
Scophthalmus aquosus	0.00	0.00	0.47	0.00

^{*} contains bass 825 mm collected from open ocean during August-September, and bass 375 mm collected during August-September from estuaries.

TABLE 5. Percent weight-of-prey items found in the stomachs of striped bass of each defined cluster and their main characteristics from the Nantucket Sound region. n_{prey} is the number of stomachs with prey.

Cluster	1	2	3
Period(s)	Both	Both	Jun-Jul
Habitat	Estuary	Ocean	Estuary
Size Interval Range (mm)	375–575	825-1 025	325
n _{prey}	89	36	5
Taxon		Percent Weight	
Polychaeta	0.27	0.08	0.00
Cephalopoda	0.05	18.41	0.00
Bivalvia	3.19	0.00	0.00
Crustacea			
Unidentified Crustacea	7.27	6.70	50.00
Squillidae	1.62	0.00	0.00
Palaemonidae	0.08	0.00	0.00
Crangon septemspinosus	14.94	0.00	0.00
Homarus americanus	7.23	2.81	0.00
Paguridae	0.24	0.00	0.00
Majidae	0.42	0.00	0.00
Cancer irroratus	7.06	1.54	0.00
Callinectes sapidus	6.78	0.00	0.00
Carcinus maenus	14.28	0.00	0.00
Ovalipes ocellatus	2.10	33.62	0.00
Mysidae	0.38	0.00	0.00
Isopoda	0.07	0.00	0.00
Amphipoda	0.00	0.71	50.00
Echinodermata			
Echinarchnius parma	0.00	0.04	0.00
Osteichthyes			
Unidentifed Osteichthyes	9.49	7.59	0.00
Brevoortia tyrannus	3.23	0.00	0.00
Fundulus heteroclitus	0.04	0.00	0.00
Menidia sp.	3.03	0.00	0.00
Gasterosteidae	0.23	0.00	0.00
Syngnathus fuscus	0.18	0.00	0.00
Triglidae	0.00	20.22	0.00
Cottidae	0.00	3.91	0.00
Stenotomus chrysops	0.00	2.23	0.00
Ammodytes sp.	17.81	2.15	0.00

Additionally, stomachs of smaller sized bass collected in August-September (clusters 1 and 3) contained higher percentages of B. tyrannus than those of larger bass (cluster 4), suggesting the consumption of H. americanus and B. tyrannus varies with the body size of bass. Likewise, in Cape Cod Bay, the diet of \leq 725 mm bass sampled from estuarine habitats during August-September (cluster 1) was dominated by B. tyrannus (53%, by weight), while the diet of larger

bass (>725 mm) taken offshore (clusters 3 and 4) contained little (0.1%) or no *B. tyrannus* (Table 6). It is difficult, however, to determine whether this pattern is size or habitat-related because smaller bass were not collected offshore and larger bass were not collected in the estuaries (Fig. 4). In the North Shore region (Table 3), the percentage of *Cancer irroratus* in the diet of \leq 675 mm striped bass from rocky habitats (clusters 2 and 3) was much higher than similar-sized

TABLE 6. Breakdown into the most important prey taxa of the diets (percent weight) of striped bass contributing to the average dissimilarity between clusters of the North Shore, Cape Cod Bay, and Nantucket Sound regions. $\overline{\delta}_{i}$ is the mean contribution of the *i*th taxon, $\overline{\delta}_{i}$ / $SD(\overline{\delta}_{i})$ is the ratio between the average contribution of the ith species ($\overline{\delta}_{i}$) and the standard deviation of the values for that species ($SD(\overline{\delta}_{i})$) and $\overline{\delta}_{i}$ % is the contribution to the total similarity scaled as a percentage. Cluster memberships are shown in Figures 2, 3, and 4 and are defined in the text. Only comparisons discussed in the text and only prey taxa deemed to be reliable discriminators are shown. Taxa proportionally more important in the diet from the first cluster of the comparison are shown in bold type.

Species	$ar{\mathcal{\delta}}$.	$\overline{\mathcal{S}}$ /SD($\overline{\mathcal{S}}$,)	$oldsymbol{\overline{\mathcal{S}}}_{i}^{}{}^{\circ}\!\!\!/\!\!\!\circ}$
	Ne	orth Shore	
Clusters 1 vs 2			
Brevoortia tyrannus	15.6	3.7	18.9
Cancer irroratus	8.2	1.8	9.9
Amphipoda	5.0	1.7	6.1
Pholis gunnellus	4.0	2.1	4.8
Crangon septemspinosa	4.0	1.6	4.8
Clusters 1 vs 3			
Cancer irroratus	8.8	2.4	14.8
Clusters 1 vs 6			
Brevoortia tyrannus	17.9	3.4	23.6
Crangon septemspinosa	10.5	1.7	13.9
Unidentified Clupeidae	5.4	2.5	7.2
Clusters 2 vs 3			
Brevoortia tyrannus	10.5	6.2	18.0
Amphipoda	4.6	1.8	7.8
Clusters 2 vs 4			
Amphipoda	5.2	2.1	9.0
Homarus americanus	4.6	1.6	8.0
Pholis gunnellus	3.4	2.0	5.9
Clusters 2 vs 6			
Crangon septimspinosa	9.8	9.0	14.2
Cancer irroratus	8.1	2.1	11.8
Unidentified Clupeidae	4.2	2.5	6.1
Pholis gunnellus	3.5	2.1	5.1
Clusters 3 vs 4			
Brevoortia tyrannus	11.4	3.7	19.6
Homarus americanus	6.3	1.8	10.8
Clusters 3 vs 6			
Crangon septimspinosa	12.5	7.7	16.5
Brevoortia tyrannus	11.9	5.9	15.7
Cancer irroratus	8.8	3.8	11.6
	Ca	pe Cod Bay	
Clusters 1 vs 2		·	
Brevoortia tyrannus	11.1 2.9	16.7	
Crangon septemspinosa		12.0	
Polychaeta	7.5	1.9	11.3
Clusters 1 vs 3			
Brevoortia tyrannus	13.5	4.3	18.5
Ovalipes ocellatus	9.1	1.7	12.5
Ammodytes sp.	5.6	1.8	7.7

bass caught in estuaries (cluster 1) suggesting that predation on *Cancer irroratus* is habitat-dependent (Table 6).

Prey Size versus Predator Size

The size distribution of prey eaten by striped bass varied widely. Fish prey ranged in size from 11 mm to 505 mm ($\bar{\chi}=67$ mm, $n=2\,806$) and crab prey ranged in size from 5 mm to 110 mm ($\bar{\chi}=29$ mm, n=906). B. tyrannus and Ammodytes sp. prey were generally ≤ 120 mm (B. tyrannus: $\bar{\chi}=62$ mm, range: 20-145 mm, $n=1\,631$; Ammodytes sp.: $\bar{\chi}=88$ mm, range: 28-206 mm, n=357) and the three dominant crab prey were generally ≤ 80 mm (Cancer irroratus: $\bar{\chi}=30$ mm, range: 5-61 mm, n=562; Carcinus maenus: $\bar{\chi}=23$ mm, range: 6-58 mm, n=194; Ovalipes ocellatus: $\bar{\chi}=32$ mm, range: 9-86 mm, n=124). Most Homarus americanus eaten by striped bass were ≤ 55 mm ($\bar{\chi}=36$ mm, range: 3-72 mm, n=40).

Significant positive relationships between mean size of prey and size of striped bass were detected for all fishes, all crabs, and the four dominant prey separately (Fig. 6). Although all of the regression slopes and most of the intercepts were significantly different ($P \le 0.05$) from zero (the exceptions were the intercepts for the 'all fishes' and 'all crabs' regressions), the regressions accounted for very little of the variability between prey size and striped bass length (most $r^2 < 0.28$). For Ammodytes sp., B. tyrannus, and Cancer irroratus, the smallest average size of animal preyed upon increased only slightly over the range of striped bass sizes examined (Fig. 6). For Carcinus maenus, the smallest and largest average sizes of animals consumed by striped bass appeared to increase linearly with predator length (Fig. 6).

Discussion

Overall, the prey taxa consumed by striped bass were similar among the coastal regions of Massachusetts. Fish and crustaceans were the dominant prey of striped bass, but their proportions in the diet varied among regions. The major fish prey were clupeids (mostly *B. tyrannus*), *Ammodytes* sp., and *Menidia* sp., while the principal crustaceans eaten were *Crangon septemspinosa*, *Cancer irroratus*, *Carcinus maenus*, *O. ocellatus* and *Homarus americanus*. Previous studies have reported similar dietary findings for striped bass (Schaefer, 1970; Manooch, 1973; Dew, 1988; Rulifson and McKenna, 1987). However, in Chesapeake Bay and Albemarle Sound, *Anchoa mitchilli* and *Leiostomus xanthurus* were found to be

important food items for striped bass (Manooch, 1973; Hartman and Brandt, 1995) but these prey rarely occur in Massachusetts waters. Many of the prey taxa in our study are associated with the benthos (Bigelow and Schroeder, 1953; Pollock, 1998), implying that striped bass – particularly in offshore areas of Massachusetts – depend primarily on benthic foraging.

Period dissimilarities in striped bass prey composition were evident in the North Shore and Cape Cod Bay regions. The disparity is primarily due to one species, *B. tyrannus*, being absent, or nearly so, from the diets of bass during June–July. The occurrence of *B. tyrannus* in the bass stomachs during August–September and the sizes of individuals consumed (30–145 mm TL) suggests that predation on this species coincides with the late summer-early autumn seaward migration of young-of-the-year menhaden from local estuaries (Nicholson, 1978; Stokesbury and Stokesbury, 1993).

Habitat-related dissimilarities in diet composition occurred for ≤675 mm striped bass in the North Shore region. The disparity in diet between fish captured in estuaries vs rocky habitats was mainly due to one species, Cancer irroratus, comprising a higher percentage of the prey of bass in the rocky areas. This pattern may result from bass in estuaries feeding on more locally abundant prey (e.g., Crangon septemspinosa) or simply because Cancer irroratus is less common in estuaries (Fogarty, 1976; Bigford, 1979). Recent DMF trawl surveys found Cancer irroratus to be very common in North Shore rocky shorelines, while Crangon septemspinosa was one of the most abundant decapods in North Shore estuaries (Chase et al., 2002).

Size-related dissimilarities in striped bass diet composition were also evident in the North Shore region. Dietary differences between small bass (<675 mm) and large bass (≥675 mm) sampled from North Shore rocky habitats were mainly due to *H. americanus* dominating the diet of the larger bass during June–July and August–September, while *B. tyrannus* dominated the diet of smaller bass during the latter period. The high percentage of *H. americanus* in larger bass suggest that these fish may select lobsters over *B. tyrannus* because *H. americanus* are easier to capture, but extensive data on predator-prey dynamics (i.e., abundances of all potential prey, selectivities, capture probabilities, etc.) are not available to support these contentions.

Previous studies of striped bass food habits indicate that individuals become more piscivorous as they grow (Bigelow and Schroeder, 1953; Schaefer, 1970; Manooch, 1973; Rulifson and McKenna, 1987; Cooper et al., 1998; Hartman and Brandt, 1995). Our findings, however, did not clearly support this conclusion. For example, we found that the diet of large bass (>675 mm) collected from North Shore rocky shorelines was dominated by crustaceans (primarily H. americanus) throughout the summer, while the diet of smaller bass residing in the same habitat changed from invertebrates to fish (primarily B. tyrannus) between early and late summer. Similarly, the dominant prey items of large bass collected from offshore waters in Nantucket Sound were crustaceans (primarily Ovalipes ocellatus) rather than fish. We therefore conclude that piscivory in striped bass is not fixed but depends upon prey abundance and availability, striped bass body size, and foraging habitat.

A food habits study of striped bass in North Carolina waters found that bass generally eat larger fish prey as they grow (Manooch, 1973). We found this to be true for both fish and crab prey consumed by striped bass in Massachusetts waters. Prey size selection theory contends that food selection in piscivorous fishes is a passive process mediated by differential size-based capture success of prey rather than active choice (Juanes, 1994). Piscivorous fishes usually select smaller prey when given a choice because smaller prey are generally "easier" to capture (due to less effective, evasive responses relative to larger prey). Our piscivory results [and those of Manooch (1973)] are concordant with Juanes' (1994) theory since the smallest average size of fish prey consumed did not change greatly as the size of striped bass increased. However, our findings with respect to Carcinus maenus prey and striped bass size (Fig. 6) are not in accord with this theory. Both minimum and maximum average sizes of Carcinus maenus increased almost linearly as striped bass size increased, suggesting bass may actively select the largest size crabs they can ingest. Such a prey-predator pattern is expected when capture success is not size-based but constrained only by predator morphology related to ingestion (e.g., gape height and throat width). Additional research is clearly warranted to gain a broader understanding of prey size selection by fishes that alternate between piscivory and invertivory.

Striped bass in the coastal waters of Massachusetts forage on several ecologically and economically important fish and invertebrate prey.

Ammodytes sp., Clupea harengus and Brevoortia tyrannus are important links between zooplankton and marine piscivores and serve as forage for economicallyimportant fishes, marine mammals and seabirds (Bigelow and Schroeder, 1953; Bowman and Michaels, 1981; Powers and Brown, 1987; Chase, 2002). The American lobster, H. americanus, supports a multimillion dollar commercial fishery in Massachusetts (Estrella and McKiernan, 1989). Striped bass may exert considerable predation pressure on lobsters given that striped bass abundance is currently at a record-high level (Anon., 2001). In fact, the Atlantic State Marine Fisheries Commission has initiated a multispecies modelling study to investigate the potential impacts of striped bass (and other fish) predation on the Atlantic coast population of B. tyrannus (Anon., 2002). However, to adequately assess the predatory impact of striped bass on their prey in Massachusetts waters, much more information is required on the abundance of prey species, prey selectivity, and striped bass consumption rates. Given the importance of striped bass and its forage species to both the ecosystem and to the Massachusetts economy, such studies should be undertaken as soon as possible.

Acknowledgements

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References

ANON. 2001. 2001 Stock assessment report for the Atlantic striped bass. Report to the Atlantic States Marine Fisheries Commission. 54 p.

- 2002. 2002 report of the Atlantic menhaden technical committee. Report to the Atlantic State Marine Fisheries Commission. 37 p.
- AYVAZIAN, S. G., L. A. DEEGAN, AND J. T. FINN. 1992. Comparison of habitat use by estuarine fish assemblages in the Acadian and Virginian zoogeographic provinces. *Estuaries*. **15**: 368–383.
- BIGELOW, H. B., AND W. C. SCHROEDER. 1953. Fishes of the Gulf of Maine. Fish Bull. U.S., 53: 577 p.
- BIGFORD, T. E. 1979. Synopsis of biological data on the rock crab, *Cancer irroratus* Say. *NOAA Tech. Rep. NMFS Circ.*, **426**: 26 p.
- BOWMAN, R. E., AND W. MICHAELS. 1981. Food habits of seventeen species of northwest Atlantic fish. *NOAA Tech. Memor.*, NMFS-F/NEC-28: 183 p.
- BRAY, J. R., AND J. T. CURTIS. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.*, **27**: 325–349.
- BRIGGS, J. C. 1974. Marine Zoogeography. McGraw-Hill Book Co., New York, NY, 475 p.
- CHASE, B. C. 2002. Differences in diet of Atlantic bluefin tuna (*Thunnus thynnus*) at five seasonal feeding grounds on the New England continental shelf. *Fish. Bull. U.S.*, **100**: 168–180.
- CHASE, B. C., J. PLOUGH, AND W. CASTONGUAY. 2002. A study of the marine resources of Salem Sound, 1997. Massachusetts Division of Marine Fisheries Technical Report TR-6. 143 p.
- CLARKE, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.*, **18**: 117–143.
- CLARKE, K. R., AND R. WARWICK. 2001. Change in marine communities: an approach to statistical analysis and interpretation, 2nd edition. PRIMER-E: Plymouth, UK.
- COOPER, J. E., R. A. RULIFSON, J. J. ISELY, AND S. E. WINSLOW. 1998. Food habits and growth of juvenile striped bass, *Morone saxatilis*, in Albemarle Sound, North Carolina. *Estuaries*, 21: 307-317.
- CORTES, E. 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. *Can. J. Fish. Aquat. Sci.*, **54**: 726–738.
- DEW, C. B. 1988. Stomach contents of commercially caught Hudson River striped bass, *Morone saxatilis*, 1973–75. *Fish. Bull. U.S.*, **86**(2): 397–401.
- ESTRELLA, B. T. AND D. J. MCKIERNAN. 1989. Catchper-unit-effort and biological parameters from the Massachusetts coastal lobster (*Homarus americanus*) resource: descriptions and trends. *NOAA Tech. Rep.* NMFS 81: 21 p.
- FOGARTY, M. J. 1976. Competition and resource partitioning in two species of *Cancer* (Crustacea, Brachyura). MS Thesis, University of Rhode Island,

- Kingston, 93 p.
- HARTMAN, K. J., AND S. B. BRANDT. 1995. Trophic resource partitioning, diets, and growth of sympatric estuarine predators. *Trans. Am. Fish. Soc.*, **124**: 520-537
- JUANES, F. 1994. What determines prey size selectivity in piscivorous fishes? *In*: Theory and application in fish feeding ecology, D. J. Stouder, K. L. Fresh, and R. J. Feller (eds.), The Belle W. Baruch Library in Marine Science 18, University of South Carolina Press, Columbia, SC, p. 79–100.
- KLEIN-MACPHEE, G. 2002. Temperate Basses. Family Moronidae. *In*: Collette, B. B. and G. Klein-MacPhee (eds.), Bigelow and Schroeder's Fishes of the Gulf of Maine, Smithsonian Institution, p. 374–389.
- LAWTON, R. P., R. D. ANDERSON, P. BRADY, C. SHEEHAN, W. SIDES, E. KOULOHERAS, M. BORGATTI, AND V. MALKOSKI. 1984. Fishes of western inshore Cape Cod Bay: studies in the vicinity of the Rocky Point shoreline. *In*: J. D. Davis and D. Merriman (eds.), Observations on the ecology and biology of western Cape Cod Bay, Massachusetts, Lecture Notes on Coastal and Estuarine Studies 11, Springer-Verlag, Inc., New York, NY, p. 191–230.
- MANOOCH, C. S. 1973. Food habits of yearling and adult striped bass, *Morone saxatilis* (Walbaum), from Albemarle Sound, North Carolina. *Chesa. Sci.*, 14: 73–86.
- NICHOLSON, W. R. 1978. Movements and population structure of Atlantic menhaden indicated by tag returns. *Estuaries*, 1: 141–150.
- POLLOCK, L. W. 1998. A practical guide to the marine animals of northeastern North America. Rutgers University Press, New Brunswick, New Jersey, 367 p.
- POWERS, K. D., AND R. G. BROWN. 1987. Seabirds in Georges Bank. R. H. Backus and P. W. Bourne (eds.). MIT Press, Cambridge, Mass.
- RULIFSON, R. A., AND S. A. MCKENNA. 1987. Food of striped bass in the upper Bay of Fundy, Canada. *Trans. Am. Fish. Soc.*, **116**: 119–122.
- SCHAEFER, R. H. 1970. Feeding habits of striped bass from the surf waters of Long Island. *NY Fish and Game J.*, 17: 1-17.
- SETZLER, E. M., W. R. BOYNTON, K. V. WOOD, H. H. ZION, L. LUBBERS, N. M. MOUNTFORD, P. FRERE, L. TUCKER, AND J. A. MIHURSKY. 1980. Synopsis of biological data on striped bass, *Morone saxatilis* (Walbaum). *NOAA. Tech. Rep. NMFS Circ.*, 433, 69 p.
- SOKAL, R. R. AND F. J. ROHLF. 1981. *Biometry*, W. H. Freeman, NY., 859 p.
- STOKESBURY, M. J. W., AND K. D. E. STOKESBURY. 1993. Occurrence of juvenile Atlantic menhaden, *Brevoortia tyrannus*, in the Annapolis River, Nova Scotia. Estuaries, **16**: 827–829.

APPENDIX TABLE 1. Number of striped bass stomachs collected from each region characterized by year, month, habitat and 50-mm length interval. 'prey' is the number of stomachs with prey and 'total' is the total number of stomachs collected.

			No. of							L	ength I	nterval											
Year	Month	Habitat	Stomachs	275	325	375	425	475	525	575	625	675	725	775	825	875	925	975	1025	1075	1125	1175	Total
										N	orth S	hore											
1997	July	Estuary	nprey		1	1				1													3
			ntotal		1	1				1													3
		Rocky	nprey		0	0	0	3	l		0	1	1	1									7
			ntotal				1	3	l		1	1	1	2									10
	Aug	Estuary	nprey			0																	0
			ntotal			1																	1
		Rocky	nprey			0		1	2	1	1	6	2	0	3	2	3						21
			ntotal			1		9	6	13	10	17	6	6	8	8	11	1					96
	Sept	Estuary	nprey			9	8	1	1														19
			ntotal			14	13	2	1														30
		Rocky	nprey				2	3	12	4	4	4	1	2	0	0	i	1					34
			ntotal				2	14	25	11	10	9	4	2	3	2	1	1					84
1998	June	Rocky	nprey			0	1	2	5	3	4	0	1	5	0	0	1		1		1		24
			ntotal			3	2	3	7	7	8	1	10	7	1	1	2		2		1		55
	July	Estuary	nprey		1	1	4								0	0	0						6
			ntotal		2	2	4								1	1	1						11
		Rocky	nprey				1	1	6	5	1	0	3	1	0	1	0	1	0				20
			ntotal				2	7	16	7	1	ı	6	4	2	4	2	2	3				57
	Aug	Estuary	nprey			1	1			1				1	0	0	1						5
			ntotal			2	1 :			1				l	2	4	2						13
		Rocky	nprey				0	8	15	6	0	0	2	0	1	2		0		0			34
			ntotal				1	14	19	15	2	1	15	5	7	3		1		1			84
	Sept	Estuary	nprey			5	6	0	1		0												12
	-		ntotal			5	8	2	2		1												18
		Rocky	nprey			1							0	0	2		0						3
		-	ntotal			1							7	3	4		1						16

APPENDIX TABLE 1. (Continued). Number of striped bass stomachs collected from each region characterized by year, month, habitat and 50-mm length interval. 'prey' is the number of stomachs with prey and 'total' is the total number of stomachs collected.

-			No. of								Length 1	Interval											
Year	Month	Habitat	Stomachs	275	325	375	425	475	525	575	625	675	725 .	775	825	875	925	975	1025	1075	1125	1175	Total
1999	June	Estuary	prey	-	2	9	9	5	3		1		2										31
			total		2	9	11	5	4		1		2										34
		Rocky	prey			3	8	14	6	4	9	4	9	5	3	3	2	1	1			0	72
			total			3	9	16	8	8	13	6	23	10	8	4	4	3	3			1	119
		Offshore	prey															1	i	2			4
			total															1	i	2			4
	July	Estuary	prey			2	6	5	1	1													15
			total			2	8	6	1	1													18
		Rocky	prey				ı	5	11	9	10	0	9	6	3	2	3	2					61
			total				2	11	20	22	26	3	21	15	4	5	6	3					138
		Offshore	prey														0						0
			total														1						1
	Aug	Beach	prey				3	4	3	2													12
			total				3	4	3	2													12
		Estuary	prey			2	4	6	4	1	1												18
			total			2	4	6	4	1	1												18
		Rocky	prey				7	5	7	8	6	1	6	2	2	4	1	3	1				53
			total				7	9	9	10	7	3	13	3	2	4	3	4	1				75
	Sept	Estuary	prey			0	4	6	3	1	1	0	0										15
			total			1	7	14	3	1	1	1	1										29
		Rocky	prey				1	9	1	1	i		1	1	1	1							17
			total				., 2	15	4	1	1		1	1	1	1							27
2000	June	Rocky	prey				5	8	17	18	12	7	3	4	1	1			1				77
			total				6	11	23	20	18	9	4	7	1	1			1				101
		Offshore	prey															2	2	1			5
			total															2	2	3			7
	July	Estuary	prey											0									0
			total											1									1
		Rocky	prey				1	5	18	26	19	8	2	13	4	0	2	4	1	0	1		104
			total				1	6	24	36	27	10	2	26	9	1	4	6	2	1	1		156

APPENDIX TABLE 1. (Continued). Number of striped bass stomachs collected from each region characterized by year, month, habitat and 50-mm length interval. 'prey' is the number of stomachs with prey and 'total' is the total number of stomachs collected.

			No. of								ength I												
Year	Month	Habitat	Stomachs	275	325	375	425	475	525	575	625	675	725	775	825	875	925	975	1025	1075	1125	1175	Total
	Aug	Estuary	prey			ı		2	10	13	3	0		1	1								31
			total			3		2	20	22	6	4		1	1								59
		Rocky	prey					4	8	12	15	9	3	14	2	2		0					69
			total					4	14	18	23	12	5	26	5	4		1					112
	Sept	Beach	prey				3	3	0	0	l												7
			total				4	4	1	1	1												11
		Estuary	prey				1	2	3	4	5	3	2	0	1								21
			total				1	3	7	5	7	5	2	1	1								32
		Rocky	prey				3	5	25	21	7	5	4	5	0	3		1	0				79
			total				3	5	27	23	8	6	6	7	2	4		1	1				93
		Offshore	prey					ì	3	2	0	0	1										7
			total					2	4	2	1	1	1										11
											Cape C	od Bay											
1997	' July	Estuary	prey		1	4	3	3	2		1				0								14
			total		2	4	3	6	5	1	1				1								23
		Offshore	prey										0	0	4	0							4
			total										1	1	5	1							8
	Aug	Estuary	prey		1				4	8	2												15
	Ü	•	total		1		.)		4	10	3												18
		Offshore	prey									0	1	1	3	2	0	1	0	2		0	
			total									1	l	5	4	4	6	4	1	3		1	30
	Sept	Estuary	prey						7	11	1	1	2		1	1	1	1	1				27
	-		total						9	14	1	1	2		1	1	1	2	1				33
		Other	prey											1		0							1
			total											1		1							2
1998	3 June	Estuary	prey	0	3	9	8	2	2	5	2	1											32
			total	1	4	12	9	2	3	6	2	1											40

APPENDIX TABLE 1. (Continued). Number of striped bass stomachs collected from each region characterized by year, month, habitat and 50-mm length interval. 'prey' is the number of stomachs with prey and 'total' is the total number of stomachs collected.

			No. of							I	ength I	nterval											
Year	Month	Habitat	Stomachs	275	325	375	425	475	525	575	625	675	725	775	825	875	925	975	1025	1075	1125	1175	Total
	July	Estuary	prey	ı	9	5	3	0	i	i	2		i				0		0				23
	,	,	total	1	12	5	3	2	3	4	3		1				1		i				36
	Aug	Estuary	prey				2		1	8	7	3	1		1				1				24
	-	-	total				2		1	10	7	3	1		1				1				26
	Sept	Estuary	prey			5	4	2	8	7	2	2	1	2	1								34
			total			5	4	2	10	10	7	3	2	2	i								46
		Offshore	prey								1	1											2
			total								2	1											3
1999	June	Beach	prey			7	7			1	1												16
			total			7	7			1	2												17
		Estuary	prey		2	6	8	4	3	1	1	ĺ		į			0						27
			total		2	10	8	5	4	2	1	1		1			1						35
		Other	prey											•	2	0	0						2 10
			total										0	2 9	4	2 10	2 8	2	٥	0			49
		Offshore	prey								1		8 15	16	9 15	13	19	3 6	0	0			88
			total			•	-		,		1	1	13		13	13	19	O	1	ı			25
	July	Estuary	prey			2 2	7 8	4	6	4	1			0			1						29
		0.001	total			2	8	6 2	1	1	1		15	6	8	9	12	3	5	2	1		68
		Offshore	prey			3	3	2	1	1			23	11	18	27	24	7	7	5			134
		D l-	total			3	3	2	1	1			23	11	10	21	0	,	,	,	~		0
	Aug	Beach	prey total				.;										1						1
		Estuary					13	6	7	3	6	3	2	0			•	2		0	0		42
		Listuary	prey total				13	10	7	7	10	5	6	2				3		1	1		65
		Offshore	prey									-	12	8	5	6	5	3	2	1	1		43
		Offshore	total										18	13	22	17	26	22	14	4	2		138
	Sept	Estuary	prey				12	15	8	3	8	5	8	0				1					60
	Sept	1.51441)	total				15	16	11	5	10	7	9	1				1					75
		Offshore	prey										2	2	1	0	1	1	1	1			9
		- 11011010	total										5	6	6	4	3	5	2	2			33

APPENDIX TABLE 1. (Continued). Number of striped bass stomachs collected from each region characterized by year, month, habitat and 50-mm length interval. 'prey' is the number of stomachs with prey and 'total' is the total number of stomachs collected.

			No. of]	Length 1	nterval											
Year	Month	Habitat	Stomachs	275	325	375	425	475	525	575	625	675	725	775	825	875	925	975	1025	1075	1125	1175	Total
2000	June	Estuary	prey		2	2	1	2	1		0		0	1	1					0			10
		•	total		3	2	2	2	1		2		1	1	1					1			16
		Rocky	prey								1	1	2										4
			total								3	1	2										6
		Offshore	prey											0	0	1	0	1	0				2
			total											1	1	1	2	l	1				7
	July	Estuary	prey			11	4	1	3	1		1											21
			total			11	4	5	8	4		2											34
		Offshore	prey						1	1	1		2										5
			total						1	2	2		2										7
	Aug	Estuary	prey		1	2	6	3		4	1												17
			total		2	2	6	3		4	1												18
		Rocky	prey				ì	2	2	7	0												12
			total				1	2	4	9	2												18
		Offshore	prey						1	0													1
			total						1	1													2
	Sept	Estuary	prey							0			1										1
			total							2	_		2										4
		Rocky	prey				1			1	5	!	!	3	0								12 13
			total				1			1	5	1	1	3	1			0					
		Offshore	prey				.)											0	2	1			2
			total															1	2	1			4
											Nantuc	ket Sou	nd										
1997	Aug	Beach	prey		1	0	7	2	3	1													14
			total		1	2	7	4	3	3													20
		Estuary	prey		1	3	4	5	6	6				0									25
			total		1	3	4	11	7	9				1									36

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APPENDIX TABLE 1. (Continued). Number of striped bass stomachs collected from each region characterized by year, month, habitat and 50-mm length interval. 'prey' is the number of stomachs with prey and 'total' is the total number of stomachs collected.

			No. of							I	ength I	iterval											
Year 1	Month	Habitat	Stomachs	275	325	375	425	475	525	575	625	675	725	775	825	875	925	975	1025	1075	1125	1175	Total
		Other	prey														0	1	2				:
			total														1	2	2				:
		Offshore	prey												3								
			total												4								
S	Sept	Estuary	prey			5	2	11	12	4	0	1											3
			total			10	4	15	18	7	l	1											5
		Offshore	prey											0	1	0							
			total											1	1	1							
1998 J	une	Beach	prey														0						(
			total														1						
		Estuary	prey		2	0	1	1	0		0												4
			total		3	1	2	1	2		1												10
		Offshore	prey									0	0	1	2	6	4	1	1		1		10
			total									1	2	4	4	8	6	4	2		1		3:
J	uly	Estuary	prey		2	4	2	l	4	0													1:
			total		3	11	3	4	6	2	_												2
A	Aug	Estuary	prey								1												
			total								1												
		Offshore	prey												1	3	3	2 2	1		1		1
			total												2	3	3	2	l		1		1:
5	Sept	Estuary	prey			2	4	3	1	1	1			0									1:
			total			4	. 4	3	1	1	1			1			0						1:
		Offshore	prey										0		Į,		0						
			total										2		1		ı						
1999 J	une	Estuary	prey											1		1							
			total											ı		2	,						
		Offshore	prey										0	l o	1	3 12	5 16	4 11	4		0		1
		_	total										3	8	4	12		11	6		1		6
J	uly	Estuary	prey		1		2	0						0			0						
			total		l		2	2						ı			I						

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APPENDIX TABLE 1. (Continued). Number of striped bass stomachs collected from each region characterized by year, month, habitat and 50-mm length interval. 'prey' is the number of stomachs with prey and 'total' is the total number of stomachs collected.

			No. of							I	ength I	nterval										-	
Year	Month	Habitat	Stomachs	275	325	375	425	475	525	575	625	675	725	775	825	875	925	975	1025	1075	1125	1175	Total
		Offshore	prey					1					1	0	0	2	0	0					
			total					1					9	11	11	13	5	2					5
	Aug	Estuary	prey						0		0		4	1				1					
			total						1		1		6	3				2					1
		Other	prey										2										
			total										4										
		Offshore	prey				1	2	0					0									
			total				1	2	1					1									
	Sept	Beach	prey															1					
			total															1					
		Estuary	prey						1	0	1	1							0				
			total						i	1	1	2							1				
		Offshore	prey													0		1	0	1			
			total													l		1	1	2			
2000	June	Estuary	prey							0	1	3	2	1	1								
			total							1	1	3	3	2	1								
		Other	prey																1				
			total																1				
		Offshore	prey									0	0										
			total									l	1										
	July	Estuary	prey			1	0	1	2	3	0		0		1		0						
			total			2	2	2	6	3	1		l		1		1						1
		Offshore	prey					0	3	2							0	0					
			total					1	7	2							2	1					i
	Aug	Estuary	prey				1		2														
			total				1		3														
	Sept	Estuary	prey															1	3	1	1		
			total															1	4	1	1		
		Other	prey														2	2	1		1	0	
			total														2	3	2		1	1	